Coordinated stasis: An overview

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Abstract

Coordinated stasis, as defined herein, represents an empirical pattern, common in the fossil record, wherein groups of coexisting species lineages display concurrent stability over extended intervals of geologic time separated by episodes of relatively abrupt change. In marine benthic fossil assemblages, where the pattern was first recognized, the majority of species lineages (60 to more than 80%) are present in their respective biofacies throughout timespans of 3–7 million years. Most lineages display morphological stasis or only very minor, typically non-directional, anagenetic change in a few characters throughout a prolonged time interval; evidence for successful speciation (cladogenesis) is rare, few lineages (<10%) become extinct, and very few new immigrant taxa become established within a region or province during such intervals. Moreover, species associations (biofacies) are nearly constant during an interval of stability, showing very similar taxonomic membership, species richnesses, dominance-diversity patterns and guild structure throughout. Conversely, during the intervening episodes of rapid change, many species (generally 70% or more) become extinct, at least locally, some lineages undergo rapid speciation and/or anagenetic change, and new immigrant taxa become successfully (semi-permanently) established. All (or most) biofacies arrays across an environmental gradient display rapid and nearly synchronous changes in various aspects, including species composition, richness, dominance and guild structure. These intervals of abrupt evolutionary and ecological change typically represent only a small fraction (<10%) of the duration of the stable units. The resulting stable blocks of species separated by turnover events comprise “ecological-evolutionary sub-units” in the Appalachian Basin type example, and are considered to be components of the longer, more generalized ecological evolutionary units (EEUs) recognized by Boucot, Sheehan, and others.

Causes of coordinated stasis and of regional ecological crisis/reorganization remain poorly understood. Tracking of spatially shifting environments appears to be the rule, rather than adaption to local change. Incumbent species appear to have a very strong advantage and may exclude potential immigrants, as evidenced by temporary incursions of exotic taxa (“incursion epiboles”); this suggests a role for ecological and biogeographic factors in maintaining paleoecological stability. Stabilizing selection may be critical for producing morphological stability in individual lineages. Episodic crises appear to involve environmental perturbations that were too pervasive and/or abrupt to permit local tracking of environment to continue. Some faunal turnovers associated with unconformities may be partially an artifact of stratigraphic incompleteness. Others, however, seem to occur within conformable successions and were evidently rapid. Widespread anoxia, changes in current patterns, and/or climatic change associated with major marine transgression are common correlates of faunal turnovers in marine habitats in the Appalachian Basin.

The phenomenon of coordinated stasis has been noted, albeit not fully documented, in a number of ancient marine and terrestrial ecosystems. An important goal for evolutionary paleoecology should be to document the patterns of
stability and change in common and rare members of fossil assemblages in order to discern the relative frequency of coordinated stasis in the rock record, to evaluate the mechanisms by which such apparent evolutionary and ecological stability might be produced, and to seek clues (e.g., paleobiological and stratigraphic patterns, geochemical anomalies) as to causes of abrupt pulses of faunal change.

Keywords: evolution; ecology/paleoecology; coordinated stasis; speciation; extinction; bioevents

1. Introduction

Nearly a century ago Herdman F. Cleland (1903) captured the essence of coordinated stasis — the near absence of change in species and in regional fossil assemblages through geologically long time spans. In the summary to his monograph on the fossil faunas of the Middle Devonian Hamilton shales of central New York, Cleland made the following remarks:

“In a section such as that of the Hamilton formation at Cayuga Lake... if the statement natura non saltum faciet is granted, one should, with some confidence, expect to find many — at least some — evidences of evolution. A careful examination of the fossils of all the zones, from the lowest to the highest, failed to reveal any evolutionary changes, with the possible exception of Ambocoelia praecumbona. The species are as distinct or as variable in one portion of the section as in another. Species varied in shape, in size, and in surface markings, but these changes were not progressive. The conclusion must be that, so long as the conditions of sedimentation remain as uniform as they were in the section under consideration, the evolution of brachiopods, gastropods, and pelecypods either does not take place at all or takes place very seldom, and that it makes little difference how much time elapses so long as the conditions of environment remain unchanged.” (pp. 90–91)

The term “coordinated stasis” was introduced by Brett and Baird (1992) to denote an empirical pattern of concurrent near-stasis coupled with synchronous abrupt change in a number of lineages and assemblages of fossils. The pattern was initially recognized in middle Paleozoic marine faunas of the Appalachian basin, particularly in Ontario, New York State, and Pennsylvania. Within the 60-million-year interval from the Early Silurian to the Middle Devonian (approximately 438–378 Ma), Brett and Baird (1995) discern fourteen blocks of coordinated stasis, each spanning some 3–7 m.y. These intervals include the well-known Hamilton-Tully fauna of the Middle Devonian (Boucot, 1990a; Brett et al., 1990; Brett and Baird, 1995), the stable nature of which was already recognized by Cleland (and Williams, 1903), as indicated above.

Within each block of stability in the Appalachian Basin, faunas of marine invertebrates (including 60–350 species of brachiopods, corals, mollusces, echinoderms, and trilobites) display a high degree of persistence from the stratigraphically lowest to highest available occurrences of their appropriate facies (Fig.1). Many species lineages display little or no morphological change over prolonged intervals, very few lineages become extinct, and few new species are added via either speciation or immigration. Furthermore, most common to moderately rare species (those making up 90% or more of individuals within assemblages) recur in predictable associations (“paleocommunity types” of Bennington and Bambach, 1996) or biofacies throughout numerous sedimentary cycles. These associations are characterized by similar species lists, guild structures, richness, dominance-diversity, and rank abundance of common taxa. The restructuring events that form the boundaries of stable units occur within geologically brief intervals and involve local extinction of widespread and abundant species, rapid evolutionary turnover, and successful immigration of “exotic” taxa.

Recently, a number of researchers have expressed interest in coordinated stasis and what it may signify (Miller, 1993; DiMichele, 1994a; Brett, 1995; Morris et al., 1995; Morris, 1995; Roy and Wagner, 1995). The pattern, if found to be widespread, carries with it a number of interesting
implications for both evolutionary and ecological theory. Because of this, and in the context of this theme issue, we feel that a broad overview of coordinated stasis and a discussion of its defining characteristics is especially needed at this time. Below, we propose an operational definition that can be consistently applied to other studies, suggest how best to test for the pattern in a stratigraphic section, review work done to date that suggests the widespread nature of the phenomenon, and discuss its macroevolutionary and ecological implications.

2. Definitions

Coordinated stasis, in its simplest form, is an expression of the bimodality of evolutionary and ecological change. This general phenomenon has been emphasized by Boucot (1975, 1978, 1983, 1986, 1990b), who recognized that patterns of stability and change in the fossil record are hierarchically organized. While his concept of Ecological Evolutionary Units (EEUs) is widely known, he has also acknowledged that these large-scale ($10^7$–$10^8$ m.y.) units are in turn composed of smaller scale subunits that display consistent groupings of species or lineages (Boucot, 1990c, 1994). Although Boucot’s (1994) EE subunits are global and often substantially longer than the regional blocks of stasis termed EE subunits by Brett and Baird (1995), several of the subunit boundaries in the Silurian–Devonian interval of the Appalachian Basin match those of Boucot rather closely. Coordinated stasis, however, was first documented and is expressed as a regional phenomenon, with intervals of stability lasting on the order of several millions of years.

The pattern of concurrent stasis and abrupt change (coordinated stasis) in mid-Paleozoic faunas of the Appalachian Basin provides the basis for recognition of many of the local stages. We draw upon these stable faunas as the type example for coordinated stasis, and suggest, based upon them, the following set of defining characteristics. We concede that the details of this definition are in some ways arbitrary, but see the value of having some specific set of properties against which to compare other concepts and data within the theme of bimodal turnover. To ensure meaningful comparisons, the definition should include the percentage of taxa persisting throughout a given interval, the proportion of taxa retained across turnover events, and the amount of time (relative and absolute) encompassed by stasis and turnover; taxonomic scale should also be carefully considered.

It is extremely unlikely that any two fossil assemblages, like any two modern communities, will ever be exactly the same, hence we must decide how much paleoecologic variability to include under the aegis of coordinated stasis. Based on the Appalachian Basin example, we tentatively define blocks of coordinated stasis as intervals, generally exceeding one million years in duration, during which 60% or more of species-level lineages persist from oldest to youngest samples of appropriate biofacies, with only minor and typically non-directional evolutionary changes. In contrast, relatively few lineages (fewer than 40% of lineages, and typically less than 20% in Appalachian Basin examples), persist across bounding intervals of evolutionary restructuring. This definition recognizes that minor morphological changes in one or a few characters may occur within lineages (e.g., reduction of the number of eye files from 18 to 16 in “Phacops rana”, but with no accompanying directional change in any other morphological character, as documented by Eldredge, 1972, and discussed by Eldredge and Gould, 1972). However, these changes represent either anagenesis or possibly cladogenesis in which the parent species rapidly became extinct, and thus result in no net increase in diversity. In saying “non-directional” we further acknowledge that morphological changes may be reversed in time. Such morphological reversal within lineages has for example been documented by Stanley and Yang (1987) and Sheldon (1987, 1990, 1996) and appears to be common within the Middle Devonian Hamilton Group (see Lieberman et al., 1995, for a quantitative example). The result can be termed “net stasis”.

Again drawing on the Appalachian Basin example, we further suggest that a block of coordinated stasis be defined as an interval of faunal stability
persisting at least 10 times longer than the pulse of change that marks its boundary. Although absolute time is difficult to measure in many ancient stratigraphic settings, relative durations of stability may be interpreted on the basis of stratigraphic scale. For example, substantial change in a fauna can be said to be abrupt if it occurs on the scale of a single biostratigraphic subzone or small-scale sedimentary cycle while adjacent faunas appear stable over 10 or more subzones or sedimentary cycles of a similar scale. A sequence stratigraphic framework can be especially useful for this purpose (e.g., Brett and Baird, 1995). Appalachian Basin faunas persist on the order of 3–7 m.y., while turnovers, where best constrained, occur within at most a few hundred thousand years (i.e., one fourth order cycle; Brett and Baird, 1995).

An important aspect of the coordinated stasis pattern is the pronounced bimodality of turnover rates. Speciation (cladogenesis), extinction, and successful immigration rates are all very low within stable blocks but peak sharply at interval boundaries. This is particularly so for common to abundant and widespread species, a general feature of the fossil record emphasized by Boucot (1990b, 1994), but at least in the Appalachian Basin it appears also to be true of many rare and/or

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Fig. 1. Stratigraphic ranges of Middle to earliest Late Devonian fossil species of two broadly defined biofacies in the Hamilton Group of west-central New York (Cayuga to Owasco Lake outcrops). Symbols for range lines: thick line—species common to dominant; thin line—species present; arcuate curves to left imply species migrated temporarily from study area down slope (south); arcs to right indicate species migrated temporally upslope (north) tracking favored environment; ●—incursion episode, brief incursion of species not normally present; o—outage, temporary absence of normally common species from appropriate biofacies. These data encompass a small subset of available Hamilton Group taxonomic ranges, and are presented from a limited geographic perspective so as to illustrate faunal tracking. Note that most Hamilton-Tully species are first recorded at the base of subunit X, track their preferred environment in unison, maintain similar relative abundances throughout, and disappear in concert at the top of the interval.

EE subunits = ecological-evolutionary “faunas” defined by Brett and Baird 1992, 1995; IX = Onondaga fauna; IXA = modified Onondaga assemblage plus unique elements of the Stony Hollow fauna; X = Hamilton-Tully fauna; XI = Geneseo fauna. Adjoining portions of subunits IX and XI are included only for comparison. Relative scale of curve is calibrated by fossil benthic assemblages (BA) as defined by Boucot (1975); note that only the deeper end of this scale is shown, with BA 3.5—diverse coral-rich offshore communities; BA 4 = diverse brachiopod communities; BA 4.5 = ambocoelid communities and BA 5 = high dominance leiochthodid communities typical of dark gray to black shale. Fossil species are subdivided roughly by biofacies into two groups: (1) those that characterize deeper water, dysoxytic areas typified by small ambocoelid, chonetid, and leiochthodid brachiopods (BA 4–5); (2) those that typify diverse brachiopod biofacies of oxic shallower, calcareous gray mudstones or argilloleaceous limestones (BA 3–4).---

Abbreviations for biostratigraphic zones include P. costatus = Polynymathus costatus costatus zone; aus = P. australis zone; koc = Tortudus kockelhannus kockelhannus zone; P. enomensis = P. xylaus enomensis zone; l., m., and n. volcanis = lower, middle, and upper P. volcanis subzones; h. c. = P. hermani–P. cristatus zones. Abbreviations for major shallowing pulses include: (for Onondaga) UM = Uppermost Moorehouse Member grainstones; TI = “Triara-B” benthonite; US = upper Seneca Member; (for Hamilton-Tully) SH = Stony Hollow (thin limestone bed in western NY); CV = Cherry Valley Limestone; HVH = Halihan Hill fossil bed; SL = Solville horizon; PK = Pekportso horizon; MV = Mottville Member; CH = Cole Hill fossil bed; DS = Delphi Station cap bed; SR = Slate Rock bed (cap Pompey Member); CF = Centerfield (Chenango) Member; ST = Staghorn coral bed; JO = Joshua coral bed; DC = Darien Center coral bed; BL = Bloomer Creek fossil bed; TT = Tichenor Limestone; MT = Menteth Limestone; RC = Rhipidomella–Centronella fossil bed; P = unnamed top Koshong phosphatic beds; BV = Bay View coral bed; TA = Tuantoon fossil beds; BC = Bellona coral bed; (for Geneseus) FT = Fir Trce fossil bed; LO = Lodii fossil bed.

Abbreviations for species: Dyaerobic Assemblage: Pac = Pacificoecia acutiplicata; Amb = Amboboeia cf. A. unobtusata; Eum = Eumamalia cf. E. pseudobolbus; Tru = Transcavalia truncata; Lon = Longipina macronota and/or L. deflexa; Dev = “Devonoehonites” scitulus; Acro = Acraspis drudendorfii; Mk = Megakozlowkaella rarocesta; Coe = Coelospira cf. C. camilla; Lept = Leptaena “thomboeidales”; Odont = Odontocrates sp. (trilobite); Ph c = Phacops cristata (trilobite); Sch = Schizophoria sp.; Var = Vaniatrina arctica; Atth = Atyrella cf. A. cora and A. spiniferae; Elit = Elitia fimbriata; Mit = Megastrophia cf. M. concava; Nae = Nucleospira aff. N. ventricosa (Onondaga) and N. concina (Hamilton); Psa = “Pseudoastrypa” sp. (Onondaga) and cf. P. devoni (Hamilton-Tully); Sph = Strophadonta cf. S. demissa; Hel h = Heliplanopterus halli (coral); Hel c = H. confluens (coral); Med = Medusospirifer cf. M. annulatus; Mac = Macrospirifer macronota; Muc = Macrospirifer consoebria; Sp 4 = Spinocyonia sp. A cf. S. granulosa (no medial notch on fold); Spi B = Spinocyonia sp. B cf. S. granulosa (deep notch on fold) — note alternation of morphotypes between A and B; Tro = Tropidoleptus carinatus; Spn = Spinatrypa spinosa; Hyp = Hypothyridina cf. H. cuboides; Ph r = Phacops rana (trilobite).
stenotopic taxa as well. Not only are speciation and extinction rates bimodal, but the magnitude of net evolutionary change that occurs in a given lineage within, versus between, stable blocks also appears to be bimodal. Species within lineages display very trivial morphological change during a block of coordinated stasis, whereas at the transition between blocks, those same lineages may display marked evolutionary changes often resulting in the assignment of new families, genera or subgenera. The combination of bimodal evolutionary change and immigration has the effect that recognizable ecological change is also bimodal (as noted in Boucot, 1990b). Despite wobbling or minor directional change in morphology, species lineages within blocks of coordinated stasis retain their characteristic positions in biofacies, as measured by relative abundance and associated lineages, until they are disrupted by crisis events associated with a boundary turnover.

Coordinated stasis as described in the Appalachian Basin is not just a phenomenon observed in a single facies, nor one observed at different times in adjacent facies (Brett et al., 1990; Brett and Baird, 1995). Stability in this case is manifest concurrently across the entire spectrum of environments present (for example, dysoxic deep water biofacies, shallow marine shelf and reef assemblages, and nearshore low diversity faunas all appear to be relatively stable at the same time). And while these different types of communities do not display the same degree of change at interval boundaries (stressed nearshore and dysoxic communities for example show considerably less turnover than do highly diverse shallow-shelf biotas), all of these biofacies appear to be affected more or less simultaneously during turnover events. Thus, it is the entire floral–faunal gradient of a particular environmental complex that exhibits stability or turnover, rather than simply a single biofacies at a time. This pervasive pattern delineates the “ecological-evolutionary sub-units” (EE subunits) of Brett and Baird (1992, 1995); see Boucot, 1990c), in which a generally similar array of biofacies persists for the duration of a stable interval, each biofacies exhibiting coordinated stasis.

The Appalachian Basin example suggests that biofacies in an EE subunit are consistent to within about 20% in (a) species richness, (b) dominance-diversity; (c) rank abundance of most common species, (d) number of guilds; (e) number of species within guilds. Moreover, guilds (or broadly defined groups of niches; cf. Bambach, 1983, and Watkins, 1991) are staffed mainly by the same or very closely related species throughout the interval. Turnover between EE subunits is rapid and synchronous, and no single unifying causal mechanism for this change can be discerned, although some bounding crises do correlate with evidence for environmental changes such as major sea level fluctuation and climatic change. While several of the EE subunit boundaries in the Appalachian Basin also correlate with previously recognized global bioevents, as already mentioned, it remains to be seen whether most locally identified EE subunits are (like EEUs) global in extent (see Boucot, 1996), or even whether coordination across biofacies occurs in other settings.

3. Taxonomic scale

Within-lineage changes may in some cases be afforded species-level status; however, there are undoubtedly inconsistencies in the degree to which these minor variants are split into distinct species. These inconsistencies reflect differences in taxonomic practices and biostratigraphic utility for the group in question. In many such cases, these minor morphological changes within lineages can be contrasted with much more substantial changes across the fauna that are associated with interval boundaries (i.e., generic-level change or extinction of lineages altogether). We argue, therefore, that clades that display species-level turnover are not exceptions to a pattern of coordinated stasis, so long as they display a pronounced and coordinated bimodality in the magnitude of their evolutionary change (allowing the recognition of blocks of relative stability). Generic level stability, despite turnover in species assemblages, has been documented for portions of Cambrian bionerates (Westrop, 1994, 1996) and benthic marine communities from the Ordovician (Patzkowsky, 1994) and Neogene (Stanton and Dodd, 1994). Boucot
(1975, 1983) also defined his "community groups" based on generic-level stability. In each case, relatively stable intervals are separated by rapid, larger-scale turnover. This, in fact, may prove to be the more general pattern, of which the pronounced species-level stability seen by Brett and Baird in the Appalachian Basin is simply a special case.

4. Documentation of coordinated stasis

Assessing the possibility of stasis first requires a comprehensive sampling strategy. Bulk sampling of fossil assemblages provides data on (at least) the abundant taxa within assemblages. Representative collections should be obtained throughout the interval, or at least from the stratigraphically highest and lowest occurrences of a biofacies. Sampling also needs to be comprehensive enough to recover rare species in the fauna, and this is not an easily resolved issue. Cobabe and Allmon (1994) suggest an approach to the problem by estimating sample sizes necessary to accurately represent abundances of different portions of the fauna. Perhaps the most effective strategy is to obtain data from large collections at numerous horizons. This may or may not be possible in certain cases, and it is very time consuming, but it is the only realistic way to determine at least the presence of rare species in different horizons. Such data exist for many of the classically studied assemblages in North America and Europe, and these well-documented faunas form a logical starting point for studies of coordinated stasis (e.g., Morris et al., submitted). In addition, classical studies of biofacies provide a wealth of information that could be tapped as initial indicators of a coordinated stasis pattern (Schopf, 1996).

To document associations and their paleoecology, assemblages must be censused and assessed in terms of ecological parameters, including: (a) species composition, (b) species richness corrected for sample size, (c) dominance diversity (Shannon-Weaver Index or others), (d) rank abundance of the more common genera and species, and, (e) trophic/substrate guild structure, (proportion of deposit feeders, suspension feeders, infauna versus epifauna, etc.). Bennington and Bambach (1996; Bennington, 1994; Bambach and Bennington, in press) stress the importance of comparing sample variation within individual sample horizons to that between horizons from the same and (ideally) additional outcrops in order to compare spatial variability in assemblage properties at a given time with temporal variability seen from one level to the next. A variety of multivariate statistical techniques have been employed to assess these properties in a fauna (see e.g., Bennington and Bambach, 1996; Holterhoff, 1996; Morris, 1996).

The morphologies of individual taxa must also be studied critically to test for the presence or absence of significant morphological change; working solely from species lists may only tell us about the dynamics of taxonomic nomenclature. The appropriate analysis of morphological change throughout a study interval of this magnitude is laborious to be sure, for a number of lineages must be studied throughout the interval in question (unlike studies testing for punctuated equilibrium in a single lineage or restricted group). Work on several Hamilton Group taxa (Lieberman, 1994; Lieberman et al., 1995) supports the claim for net morphological stasis among co-occurring species (Lieberman and Dudgeon, 1996). The basic guidelines for carrying out such a study, as well as initial results, are outlined by Morris (1994, 1996). Several earlier studies of morphological variation through time, originally designed to test the model of punctuated equilibrium in single lineages, also coincidentally show simultaneous speciation and probable linked stability in a number of lineages (Williamson, 1981; Cheetham, 1986, 1987; Jackson and Cheetham, 1994). Admittedly, most morphometric studies to date have involved common taxa. Boucot (1990c) has asserted that rare taxa should display more significant evolutionary change than those that are common. There are obvious problems in obtaining samples of rare species large enough to allow for statistically significant morphological analysis, hence Boucot's hypothesis remains to be critically tested. Observations of long-ranging rare species in the Devonian of New York, however, do not reveal evidence for substantial change. For example, Lieberman's (1994) study of the rare proetid trilobites *Basidechenella*
rovi and Monodechenella macrocephala in the Middle Devonian Hamilton Group indicates near identity at all levels.

Lastly it is valuable, though not essential, that a time series be sufficiently long as to encompass the possibility of not only an interval of coordinated stasis, but a turnover event as well. In situations where range data are available for a number of coexisting taxa throughout a significant period of time, it may be possible to test for the likelihood of coordinated stasis by looking for bimodality in the rate of turnover. This approach has been attempted by Alroy (1996) and yielded negative results (in this case, for Cenozoic mammals of North America). This method may be compromised if not all the biofacies encompassed by the data exhibit coordinated stasis, or if mixing of biogeographic zones has inadvertently occurred in tabulating data. It would be a useful exercise to apply Alroy's method to sections where coordinated stasis has already been independently demonstrated to test the statistical "strength" of the bimodal signal.

5. Artifacts and biases: Potential confounding factors

Two sources of bias in the fossil record may produce a false appearance of coordinated stasis and thus should be anticipated in the interpretation of any particular suite of fossil distribution data. The first, explicated by Holland (1994, 1995, 1996), is the truncation of fossil range data by sequence boundaries. Specifically, Holland suggests that not only can the effect of missing time at an unconformity create the illusion of pulsed turnover, but that major facies shifts associated with sequence boundaries and transgressive surfaces (regardless of whether or not time is missing) can produce a similar effect. This potential artifact can be ruled out with geographically widespread data sets in which it is possible to trace lateral shifts of a given biofacies within precisely correlated stratigraphic intervals, as has been done to some degree with the Appalachian Basin faunas (e.g., papers in Brett, 1986, and Landing and Brett, 1991; Brett and Baird, 1995). If, however, major unconformities occur at boundaries between apparently stable faunas, it may not be possible to determine whether or not a pattern of simultaneous change in many lineages is real or merely artificial.

Some of the known intervals of coordinated stasis appear to have their boundaries in relatively conformable successions. The boundaries of at least six EE subunits (blocks of gradient-wide coordinated stasis) in the Appalachian Basin occur not at erosional sequence boundaries, but rather associated with highstands in conformable, if also somewhat condensed, successions of dark gray and black shale facies (Brett and Baird, 1995). Moreover, a number of these blocks of stability contain within them sequence-bounding unconformities of considerable magnitude. For example, the Hamilton-Tully fauna in the Appalachian Basin contains a major (second order) sequence boundary (Taghahic unconformity of Johnson, 1974, which separates the lower and upper halves of the Kaskaskia supersequence; Sloss, 1963). Typical Hamilton species, as well as characteristic biofacies, recur in the upper part of the Tully Limestone well above this unconformity. Hence, relatively large unconformities are commonly not associated with EE subunit boundaries; such boundaries are commonly present in other parts of the sedimentary cycle, such as highstand or transgressive systems tracts. Furthermore, even though unconformities may impart an artificial coincidence to the beginnings and ends of species ranges, they can not account for the persistence of similar assemblages of species and the paucity of evolutionary change within bounded sequences.

A second possible pitfall in the identification of coordinated stasis involves the notion of "taphonomic mirage", as suggested by William Miller (1993, 1994, 1996). Miller cautions that certain recurring fossil assemblages may merely represent taphofacies. In other words, consistent preservational conditions associated with persistent sedimentary environments may favor preservation of only certain members of original communities. If those members also happen to be long-ranging taxa, a mirage of coordinated stability could be the result (see also Westrop, 1996). Taphofacies are a reality and taphonomic processes may select for robust or insoluble skeletal elements. However,
taphonomic bias alone cannot explain distribution patterns such as those common in the Hamilton Group wherein different associations of taphonomically equivalent species recur in distinct but sedimentologically similar facies. For example, among similar sized calcitic brachiopods, differential taphonomic processes could not possibly produce the marked differences in species assemblages observed among varied Paleozoic mudrock facies within particular EE subunits. Taphonomic mirage can generally be ruled out, especially if the assemblages involved are relatively diverse and well-preserved.

Miller (1994, 1996) has also distinguished between what he sees as coordinated stasis sensu stricto and the concept of “structural continuity” in which taxonomic staffing and functional categories (guilds) tend to recur predictably when similar habitats happen to appear, without spatiotemporal continuity of specific associations (see also Bennington and Bambrick, 1996). Coordinated stasis, defined as a pattern of shared morphological stasis in many lineages and of recurring biofacies, does not specify that species associations must persist without any change. Indeed, species associations or biofacies may recur either because they persist as tracking assemblages or because similar associations of species reassemble in similar environments without actual temporal continuity. Neither pattern is specified or precluded in the present definition of coordinated stasis, although their ecological implications differ.

So long as the same species lineages are involved in the recurring assemblage, Miller’s structural continuity would be encompassed (in part) within this concept of coordinated stasis. Apparent examples of both phenomena have been reported in the literature (Brett and Baird, 1995; Holterhoff, 1996; Bennington and Bambrick, 1996; see Schopf, 1996, for discussion). Without good geographic and paleoenvironmental control, it will be impossible to distinguish between these two possibilities. A strong indication of persistence and tracking, however, is provided by recurrent appearances of highly stenotopic taxa in specific facies and associations. Because these species only occur in single environments, it would seem that those particular conditions must persist somewhere throughout the entire range of the stenotope species to prevent extinction of the species (but see Holterhoff, 1996, for an alternative).

6. Generality of the pattern

The notions of coordinated stasis and ecological evolutionary subunits were founded in large measure on the basis of the well preserved fossil record of marine invertebrates from the mid Paleozoic (Brett and Baird, 1995; Boucot, 1994; Fig. 1). Recently, however, a number of researchers have reported findings suggestive of coordinated stasis from many disparate ecological settings; many of these studies are published in this theme issue. Below, we briefly review the spectrum of environments from which this or similar phenomena have been reported (see also Boucot, 1996). It should be noted that the studies chosen to illustrate pattern in different settings by no means compose an exhaustive account of relevant work in these areas; rather they represent a sub-sample heavily weighted toward work in this theme issue. These case studies indicate that the pattern of concurrent morphological stasis and ecological stability at the scale of coordinated stasis is neither unique to the middle Paleozoic, the Appalachian Basin, nor to marine benthic biotas.

6.1. Marine benthos

A number of studies have now documented patterns of coordinated stability and change in various marine invertebrate ecosystems ranging from the Cambrian to the Neogene. Two well documented examples of stasis at the species level are provided in papers by Bennington and Bambrick and by Holterhoff in this issue. Bennington (1993, 1994; Bennington and Bambrick, 1996) presents work on recurrent assemblages in four successive marine tongues within a dominantly nonmarine fluvial deltaic successions in the Pennsylvanian of Kentucky. Using cluster analysis to characterize faunas, he is able to demonstrate a considerable degree of similarity amongst faunas that differ in age by as much as 10 m.y. Similar species lists and even similar rank
abundance of common species characterize all four major cycles. Although detailed studies reveal small but statistically significant differences among faunas (largely owing to variations among rare taxa), on the whole we find that Bennington’s study provides one of the best documented cases for general continuity of lineages and similar recurring assemblages.

The study by Holterhoff (1994, 1996), also in the Pennsylvania, examines a number of crinoid biofacies in cyclothems of the North American midcontinent. He, too, is able to identify a number of internally consistent assemblages that persist through major changes in sea level. His work will also shed light on the question of faunal tracking versus disintegration and reassembly of faunas, for one of his biofacies apparently occurs only in the transgressive portions of his three sea-level cycles, while it is absent from the corresponding regressive portions. He implies that the biofacies, lacking a refugium, is reassembled from the “species pool” de novo each time the environment is present, making it all the more interesting that cyclic reassembly should repeatedly produce this “same” biofacies (see Schopf, 1996). Some degree of uncertainty will always remain, however, about whether this biofacies may have persisted elsewhere in a refugium during the intervals in which it has not been found.

Another set of studies has revealed species level stability and rapid turnover in the marine realm, in this case for reef corals in the late Cenozoic. Jackson (1992) has demonstrated pronounced stability in Caribbean reef coral community zonation and composition for the last 2 million years, despite large climatic and sea-level changes associated with Plio-Pleistocene glaciation. Budd et al. (1994) have extended this pattern back into the Miocene, documenting long term fauna-wide stability punctuated by a rapid turnover event at roughly 8 Ma. They have been able to collect information on the geographic expression of the turnover episode, and interestingly, while the turnover occurs in the same way at each site in the Caribbean, each locality across the region apparently experiences turnover at a slightly different time (Budd and Johnson, 1995). Their work will be crucial to understanding the mechanisms of ecosystem disintegration and the establishment of new stable states.

A number of other studies from marine settings, while observing continual turnover at the species level, have been able to demonstrate patterns of coordinated stasis at the generic level. As discussed above, we believe such patterns may be expressions of a phenomenon similar or identical to that seen at the species level in other cases. Cambrian trilobite biormes are the best example of this situation. Biomeres, as defined by Palmer (1965, 1984), bear numerous resemblances to the EE subunits of the Silurian and Devonian Appalachian basin (Brett and Baird, 1995). They display persistent and recognizable biofacies characterized by similar suites of morphologically consistent trilobite genera (particularly in later phases of biormere development; Westrop, 1996), separated by sharp boundaries at which there is substantial extinction of long-lasting lineages followed by rapid evolutionary and immigational turnovers. There is, however, considerably more turnover at a species level within these biromes than in the stable faunas of the middle Paleozoic (Westrop, 1994, 1996). Westrop (1996) suggests that the more rapid species level turnover may be a consequence of the higher volatility (sensu Gilinsky, 1994) of Cambrian trilobites compared with later Paleozoic clades, as Foote (1988) has shown relative to Ordovician and later trilobites. We maintain that so long as this turnover is within lineages and biofacies retain their distinctive character over the interval, the bimodal signature of coordinated stasis may be manifested here at the generic level.

Similar scenarios are described by Patzkowsky (1994) and Stanton and Dodd (1994). Patzkowsky (1994) has documented two intervals of about 15 m.y. each in the Middle and Late Ordovician of eastern North America during which brachiopod biofacies remain stable. Again many genera, but not species, persist in similar associations. These intervals are inferred to represent prolonged environmental stability terminated by abrupt paleo-oceanographic shifts. Stanton and Dodd (1994) also describe generic level stability in molluscan associations from the Neogene of California despite considerable species-level change.
6.2. Terrestrial plants

Very similar patterns of morphological stasis and stability of associations of plant species have also been documented for Carboniferous flora (Wing, 1984; Raymond, 1993). In particular, DiMichele and Phillips (1992, 1995, 1996); DiMichele, (1993, 1994b) have documented that persistent assemblages of coal swamp plants display similar ecomorphic guilds filled by the same or closely related species for up to 9 million years. These florals, like the faunas in the Appalachian Basin, show tracking in response to environmental change and stability across the entire “landscape”, or biofacies gradient.

6.3. Terrestrial animals

Early indications that some terrestrial vertebrate communities may display coordinated stasis came from Olson (1952). His account of Permian vertebrate “chronofaunas” reports a pattern of long term stability in vertebrate associations separated by brief intervals of turnover and reorganization. Later, Vrba (1995) described antelope faunas from Africa that also display comparably long intervals of morphological stasis and ecological similarity punctuated by rapid change. These observations provide the basis for her “Turnover-Pulse Hypothesis”. Prothero (1994; Prothero and Heaton, 1996) has demonstrated the persistence of many Western Interior mammal species through climatic crises associated with the Eocene–Oligocene boundary, potentially indicating some form of resistance to disturbance events by the fauna. Barry et al. (1995) report intervals of relative faunal stability in mammal assemblages from the Neogene Siwaliks in northern Pakistan. Even the North American Land Mammal Ages used in Cenozoic biostratigraphy display staffing of persistent guilds by the same or related species for periods of up to 10 million years (Woodburne, 1987; Prothero and Berggren, 1992). Some invertebrate assemblages on land may also exhibit a pattern of coordinated stasis and change, as Morris (1994, 1996) suggests based on preliminary studies of gastropods from Pliocene rift basin faunas in Zaire.

6.4. Microfossil assemblages

Three recent studies of benthic foraminiferal assemblages from the Palaeogene suggest that coordinated stasis may be expressed in these communities as well. Gaskell (1991), McGowran (1987), and McKinney and Frederick (1994) all report intervals of persistent or recurrent stable associations separated by brief intervals of turnover in, respectively, the U.S. Gulf Coastal Plain, Southern Australia, and the U.S. Atlantic Coastal Plain. McKinney and Frederick (1994; McKinney et al., 1996), however, caution that this pattern may only be characteristic of the more common taxa in an assemblage. This is a point that deserves further consideration with respect to other studies as well (see Boucot, 1996).

Lastly, there are even suggestions of some form of coordinated stability in the plankton. Lu and Keller (1994, 1995) document three intervals of relative faunal stasis in Paleocene–Eocene planktonic foraminiferal assemblages from the Tethys region. Steady levels of species richness and low rates of species turnover characterized the stable intervals, and these were terminated by brief (200–400 k.y.) intervals of rapid turnover. Stability persisted despite fluctuations in temperature indicated by oxygen isotopic values, and turnover at least in one instance seems to correlate with large scale climatic change.

6.5. Counterexamples

Hence, a wide array of studies from diverse ecological settings and varied taxonomic groups seem to demonstrate comparable patterns that might be consistent with our definition of “coordinated stasis”. There are a number of studies, however, that appear to show contradictory patterns for long-term community behavior. Most commonly cited are the many studies from the Pleistocene and Holocene, where high resolution work has been able to decipher biogeographic changes for individual taxa on the scale of $10^2–10^4$ yr (e.g., Huntley and Webb, 1988, 1989) for terrestrial plant communities based on pollen records, and Valentine and Jablonski (1993) and Roy et al. (1995) for western North American
marine mollusk assemblages). Such studies report continual change in community composition governed by individualistic responses and reaction lag times of taxa to environmental change. Boucot (1983, 1990b) reviewed this apparent departure from the apparent stability of more ancient marine communities and termed it the "Pleistocene Paradox". While these studies are certainly telling us something about the last 125,000 yr, we question the comparability of short-term, high resolution studies during a period of glaciation and rapid climate fluctuation to the longer term studies of coordinated stasis in the fossil record (see also the review in Schopf and Ivany, in press). Time averaging in the fossil record may serve to filter out such high frequency variation and reveal an equally meaningful longer-term pattern. Boucot (1990b) also makes this point, and adds that marine benthic communities were likely more "buffered" against the severe short-term climate fluctuations that so affected the terrestrial systems from which most of these inferences are drawn. It should also be remembered that intervals of turnover in the mid-Paleozoic Appalachian Basin persisted on the order of tens- to hundreds-of-thousands of years, comparable to the entire duration of intervals encompassed in these more recent studies.

Another recent paper that could be cited as a counter to coordinated stasis is the Buzas and Culver (1994) study of benthic foraminiferal assemblages from the Tertiary Coastal Plain of eastern North America (see, e.g., Jackson, 1994). These authors tallied benthic foraminiferal assemblage composition for each of six transgressive intervals and examined immigration/emigration, speciation/extinction, and persistence of foraminiferal species between each interval. From their results they were able to conclude that assemblages in each successive interval were very different from one another and therefore did not support migration of a coherent ecological association in response to sea-level change. The analogy to studies of coordinated stasis, however, breaks down when one considers the scale at which this study was done (see Schopf and Ivany, in press). Foraminiferal assemblages for a given transgressive interval in this case represent a single list of taxa present during any part of that interval, each of which encompasses 2–8 m.y. There are no data for times between successive transgressions, hence there are gaps of up to 24 m.y. for which no information is recorded. Were coordinated stasis to be present in this setting, it would unquestionably be missed by the sampling strategy employed by Buzas and Culver. In fact, were the Appalachian Basin faunas to be sampled in a similar way, the results would be the same as those seen in the foraminiferid study because only a single sample from each of the intervals of coordinated stasis (EE subunits) would be available for comparison. The Buzas and Culver study is valuable for examining the restaffing of assemblages from the overall species pool following large scale, long-term sea-level change. Using this paper as a counter-argument to coordinated stasis, however, would be unjustified unless the authors are able to resolve changes in assemblage composition within each successive transgressive interval.

6.5.1. Macroevolutionary implications

Coordinated stasis appears to be a common phenomenon that characterizes fossil faunas in widely different paleoecological settings. A number of constraints on the modes of large scale evolution would seem to be imposed by the pervasiveness of this pattern. We contend that coordinated stasis runs counter to expectations of many traditional evolutionary models, including those of the Modern Synthesis (Dobzhansky, 1937). The pattern indicates that stability is the norm throughout life's history and that evolutionary change is rare and discontinuous. Moreover, and echoing the claim of Boucot (1990b), the pattern indicates that both significant morphological change within organisms and major ecological restructuring occur in a very small proportion of earth's history, perhaps less than one percent of geologic time. Many long-standing ideas about the mechanisms of large scale evolutionary change must be reconsidered in light of this widespread pattern of stasis.

6.5.2. Diversity trends

A trend of progressively increasing taxonomic richness through the later Mesozoic and Cenozoic has long been recognized within the marine fossil record (Valentine, 1973; Sepkoski, 1978, 1981).
Similarly, an increasing number of guilds of benthic organisms was documented by Bambach (1975). Nonetheless, empirical studies of Mesozoic and Cenozoic marine communities indicate that species number, guild structure, and generic, if not actual species identity, may be maintained through long blocks of time (see Dockery, 1986; Gaskell, 1991; Stanton and Dodd, 1994; Tang and Bottjer, 1995). Thus, such long-term trends must not always arise as a result of continuously ongoing processes, but may also be the net result of a series of stepwise changes.

Species packing models might predict that following a turnover event communities would begin with a small numbers of species and then gradually accumulate a number of additional species over an interval of several million years. Aside from the Cambrian bioteres, there is little conclusive evidence that communities display this predicted buildup in diversity throughout an ecological evolutionary subunit or EEU (Boucot, 1983, 1990b). Observations suggest that within an interval of stability a fixed number of guilds as well as a nearly constant number of species within guilds is maintained for the duration of the interval. The observation of nearly identical species diversities within communities at the beginnings and ends of blocks of stasis provides a strong challenge to the notion of the “ecological wedge”, originally formulated by Charles Darwin and later recast in the form of the Red Queen hypothesis (Van Valen, 1973). There is little or no fossil evidence to justify the notion of species packing during long intervals of geologic time. Rather, particular guilds appear to be filled early during restructuring events and to remain filled by the same species or at least by the same lineages with only very minor species level changes (see Sheehan, 1992, 1994, 1996).

6.5.3. Escalation

Notions of progressive change in marine communities, such as the Escalation Hypothesis proposed by Vermeij (1987), typically imply a pattern of continuous competitive struggle and intensification of interactions through geologic time. However, as with the Red Queen hypothesis, the scale at which most previous studies have been done (e.g., Vermeij, 1977, 1987; Signor and Brett, 1984) makes it impossible to test for continuity versus episodicity of process. Authors have documented general trends in increasing stereotypy or increasing frequency of interactions that demonstrate a type of escalating process. The question, however, remains as to whether or not this type of intensification is ongoing during most of geologic time. The direct fossil record of organismal interactions, including predation, documented in the numerous case studies compiled by Boucot (1990b) suggests quite the opposite. Organism interactions appear to arise abruptly and then to persist for long periods of time within coevolving lineages, even across times of major crisis. However, few attempts have been made to test on a fine scale whether escalation, when it occurs, takes place in a quantum, step-like pattern or through a gradually intensifying process (but see Kelley and Hansen, 1993; Hansen and Kelley, 1995).

Very preliminary data on interactions within blocks of stability in the Appalachian Basin suggest that there is very little escalational change in organismal interactions throughout intervals of several million years (see also Morris, 1996). For example, drill holes of a predatory gastropod-like organism appear in Middle Devonian brachiopods near the beginning of the Hamilton fauna; comparison of brachiopod samples through the upper two thirds of the Hamilton Group indicates similar frequencies of attack and similar prey selection throughout the group (see Smith et al., 1985). The evolution of new organism interactions must involve some type of restructuring of local community dynamics; however, once established these types of relationships appear to become stabilized and to remain constant through extended intervals (Boucot, 1990b). Thus, we suspect that the “escalation” of interactions, such as that observed in the “Mesozoic Marine Revolution” and/or the “Paleozoic Precursor” to that revolution (Signor and Brett, 1984) actually involves a series of discrete steps timed with the restructuring events that bound intervals of stability. During the rest of geological time, organism interactions may be in a state of near equilibrium.

Is there a constant struggle for survival and an
ever-escalating arms race that marches continuously through time? The data of coordinated stasis strongly suggest that the answer is no. This raises a key issue with regard to the role of interspecific competition in large-scale evolution. If competition is strong and constant among species in a community, the expected result would be continual escalational change; this is demonstrably not the case. One possibility is that competition is minimal during most of geologic time, being only intensified during times of crisis; thus, there is normally no selection pressure for escalation or increased diversity. Alternatively, interspecific competition is intense during most of geologic time, but only between resident members of a community and potential newcomers; this would prevent successful immigration of exotic taxa as well as the establishment of newly formed species. Both of these hypotheses are consistent with a pattern of nearly complete ecological and evolutionary stasis within biofacies. However, the resilience of established communities to introduction of new species seems to favor the second alternative (see Ivany, 1996). Extinction brought on by environmental disruption may relax this competition, permitting the evolution of new and more complex ecosystem dynamics.

6.6. Ecological implications and possible sources of stability

6.6.1. Non-invasability

The implications of coordinated stasis for ecology are striking. Many neo-ecologists have favored a pattern of more or less continuous change and contingency within communities (Gleason, 1926; Bush et al., 1992). In other words, local communities represent little more than temporary collections of species that happen to be able to live together at a particular time and place. A corollary of this individualistic view is that membership in such loosely structured communities should not be highly constrained. Yet, coordinated stasis in the fossil record demonstrates that species membership in individual biofacies may be nearly constant for vast periods of time; there is very little immigration, emigration or extinction except at the ecological evolutionary subunit boundaries. Where careful search has been made for rare species within the Appalachian Basin EE subunits, fewer than 10% of lineages were found to terminate within a block of stability (Brett and Baird, 1995). Likewise, relatively few new immigrants are noted within an interval, and even fewer of these “late” arrivals become established as permanent parts of the tracking fauna. The observation of incursion epiboles is relevant here. These are thin (centimeters to a few meters), but geographically widespread, stratigraphic intervals in which a species normally absent from a particular region is present or even transiently dominant (Brett et al., 1990). In some instances the source of the immigrant species can be identified in another biogeographic province or region (Brett and Baird, 1995). It is evident, therefore, that species are capable of invading communities under special circumstances, yet despite their widespread distribution during such episodes, these taxa disappear from the record as abruptly they appear, being replaced/displaced by members of the original community (Fig. 1). This evidence demonstrates that resident communities were generally refractory to permanent new introductions. Hence, epiboles provide a natural experiment indicating that locally established biotas, consisting of widespread abundant species, are quite stable on time scales of hundreds-of-thousands to millions of years even in the face of biotic change. Only during times of major crisis or turnover do large numbers of immigrant species become successfully (i.e., permanently) established within a particular region.

Non-invasability of communities in local ecosystems is also suggested by the fact that contemporary biogeographic provinces may coexist even in the absence of distinct geographic barriers. For example, in the Devonian of the Eastern Americas Realm, two distinctive biotas exist side by side, the Michigan Basin fauna, and the typical Appalachian Basin fauna (Imbrie, 1959; Oliver, 1977; Eldredge, 1972, 1974; Brett, in prep.). Despite similarity in family and generic level composition in comparable facies, these two areas maintained distinct suites of species (and many genera) throughout more than 10 m.y. of Middle Devonian time. These two regions were in close proximity throughout this time and do not seem
to have had geographic barriers separating them during much of the interval, although subtle temperature differences might have helped to maintain the boundary. Presumably, distinctive suites of species were established during times of isolation, perhaps associated with sea-level lowstands. The discreteness of their faunas was maintained even during times of highstand when the free exchange of larvae would seemingly have been possible between these two adjacent regions. Similarly, Hallam (1978) documents that among ammonoids and belemnoids the Jurassic Boreal and Tethyan Realms remained distinctly separated along a rather sharply defined "border", despite the apparent absence of a physical barrier.

6.6.2. Role of interspecific interactions in maintaining stasis

These observations do not imply that communities are superorganisms. Indeed, the fact that species show differing ranges along particular environment gradients, the occurrences of epiboles and outages (absenteeism of normally common taxa) (see Fig. 1), and slightly shifting dominance positions within members of biofacies, all argue that communities as rigid semi-permanent entities do not exist. Despite this, there do appear to be rules of membership that apply to biofacies during vast intervals of geologic time.

We suggest that the degree of exclusivity and non-invasibility exhibited in biofacies arranged along environmental gradients implies an important role for biotic interactions in the maintenance of faunal stability. Some form of internal coherency appears to be necessary to maintain the stability of assemblages (derived from either traditional notions of incumbency, or ecosystem organization e.g., ecological locking of Morris et al. (1992, 1995) or structural hubs of Miller (1996); see discussion in Ivany, 1996). Only during times of disruption and turnover is this constraint relaxed, the general structure of biofacies broken down, and a wide array of restructuring processes allowed to take place. Individualist dynamics such as those documented frequently by neo-ecologists likely prevail at these times. Niches or guilds become temporarily vacated as a result of extinction or possibly emigration. These can be filled with locally derived new species, by extensions of ranges of surviving taxa, or by new immigrants. Such a situation may exist for geologically brief intervals ($10^4$–$10^5$ yr; see Lu and Keller, 1994, 1995) or for somewhat longer intervals following major mass extinctions (see Westrop, 1994, 1996; also Sheehan, 1996). The late Pleistocene–Holocene interval may represent one such time of crisis and restructuring, rather than the norm of stability that prevailed during most of geologic history (see also DiMichele, 1994a; Schopf and Ivany, in press).

Depending upon the availability of species for refilling of guilds, a few species may come to occupy broadly defined niches or a large number of species may partition available resources. Regardless, this partitioning appears to occur relatively rapidly following an environmental crisis, and there is little opportunity for reorganization of biofacies after the initial phase of reestablishment. Expansions of species' niche breadths to encompass new environments appears to occur only at these times, lending further support to the hypothesis of biological influence on stability. For example, the orthid brachiopod *Tropidoleptus carinatus* occurs exclusively in nearshore sandy environments during the Early Devonian, but extends to offshore mudrock facies by Middle Devonian time (Boucot, 1975). This observation suggests that taxa may be physiologically capable of living in environments other than those in which they are typically found, but over long intervals of time they are constrained to particular biofacies. Moreover, at certain times entire guilds appear to remain unfilled following an ecological crisis. For example, following a major late Middle Devonian Givetian crisis in the Appalachian basin phacopid trilobites, which had been abundant and widespread in a number of biofacies during the preceding interval, virtually disappear and do not re-emerge in the appropriate biofacies or environments. Were the guilds filled by soft bodied, non-preservation organisms or did they merely remain unfilled for lack of suitable replacements?

6.7. Boundary events

Given the evident stability of species and species assemblages over profound periods of geologic
time, an obvious question is what are the processes in earth history that serve to break down stable faunas and permit invasion, not only by immigrant species from other areas or provinces, but also by new species produced in peripherally isolated populations? A number of factors must be considered in any attempt at explanation of the boundary intervals. First, although certain ecological crises may be local, a number of ecological evolutionary subunit boundaries appear to correlate approximately in time in widely separated parts of the world. For example, the majority of EE subunit boundaries recognized in the middle Paleozoic of the Appalachian Basin region are also recognizable in western Europe, Bohemia, Morocco and the Gondwana continents (Boucot, 1990a, 1996). In addition, one of the three “saltational” episodes (turnovers between stable intervals) recognized by Lu and Keller (1994, 1995) in late Paleocene foraminiferans also appears to be a globally recognized climatic change event. Hence, at least some ecological evolutionary subunit boundaries correspond to global bioevents (see also Boucot, 1983, 1990b, 1994; papers in Walliser, 1996). Strictly local physical factors, such as basin tectonics and orogenesis, or biotic disturbances such as disease epidemics therefore appear less likely as ultimate causal factors than do global perturbations such as climatic warming and cooling or major changes in circulation patterns or eustatic sea level. Marine and terrestrial ecosystems were not invariably affected simultaneously, although recently Algeo et al. (1995) have argued that major Devonian anoxic events and marine biotic crises might be genetically linked to episodes in the evolution of land plants. Moreover, it is apparent from the Appalachian Basin studies that varied marine environments may all display a response to the same disturbance.

No single factor seems to coincide with all EE subunit boundaries in the Appalachian Basin. Major sea level drops producing sequence-bounding erosion surfaces appear less tightly correlated with EE subunit boundaries than do major highstands; widespread anoxia associated with major transgressions appears to correlate with several boundaries. However, the sea level rise and/or anoxia may themselves be secondary effects associated with other factors of greater importance such as global climatic warming (see also Patzkowsky and Holland, 1993). Circumstantial evidence from the pathways of immigrant faunas suggests that changes in local temperature conditions accompanied some of the boundaries. Similarly, for terrestrial communities, episodes of abrupt climatic change such as warming, cooling, or the development of more arid conditions seem to correlate with radical changes in local community structure and accelerated rates of extinction and evolution (Vrba, 1985; Kerr, 1992).

Unfortunately, at present most EE subunit (and coordinated stasis) boundaries appear sufficiently abrupt and incompletely recorded that the details of environmental change associated with these ecological and evolutionary restructuring events will remain obscure. Still, in the most continuous sedimentary sections associated with local depocenters, it may be possible in some instances to resolve the fluctuations that are associated with these drastic turnovers (Budd et al., 1994; Morris, 1994, 1996). Furthermore, for the larger extinction events such as the bioregion boundaries of the Cambrian, the restructuring interval may be more prolonged, thus permitting a more detailed observation of processes (see Westrop, 1994, 1996; Sheehan, 1994, 1996).

The recent emphasis on recovery from extinctions (Harries, 1995) might also produce valuable insights into these processes. EEU boundaries generally correlate with mass extinctions (Sheehan, 1996) and thus these events must also truncate constituent EE subunits. The expansion of mass extinction studies (see Allmon and Morris, 1995) to include recovery periods and the establishment of new stable faunas may thus be the most promising avenue for insights into the development of coordinated stasis in faunas (see Sheehan, 1996).

6.8. **Prospectus**

The observation of periods of earth history characterized by coordinated stasis challenges a number of assumptions underlying traditional evolutionary and ecological models, but research into
this pattern is still in its infancy. Many questions are raised by the preliminary data of those studies which have been carried out: How pervasive is coordinated stasis? Is it more characteristic of certain times in Earth’s history than others? Has there been a tendency for coordinated stasis to be damped through time? (Or the reverse? — see Westrop, 1996.) Is it, for example, more prevalent in the mid Paleozoic than in the Mesozoic or Cenozoic times? Is it more typical of some ecological settings than others? What are the causal factors of prolonged intervals of shared stability, not only in species compositions and morphologies but in organismal associations? What causal factors result in the breakdown of intervals of coordinated stasis? What is the specific pattern of redevelopment of biofacies and species following these events?

These and other questions provide a critical agenda for evolutionary paleoecologists. Above all, many more case studies must be carefully documented before we can attempt to fully model the circumstances involved in this possibly widespread evolutionary-ecological pattern. This theme issue is the beginning of such an effort. Ultimately, the documentation of coordinated stasis and the need to account for the mechanisms that generate this pattern may lead to a new synthetic view of the evolutionary process which integrates the processes of species evolution, ecology, and mass extinction. Therein lies the most significant goal and challenge of evolutionary paleoecology.

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